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Animal Vision: Starfish Can See at Last

Starfish have small compound eyes at the ends of their arms. Until recently no behavioural function had been found for them, but now it appears that starfish are able to use them to navigate to the edges of reefs from which they sometimes stray.

Michael F. Land

Although starfish are deuterostomes, and so are our very distant relatives, their compound eyes are quite unrelated to the single-chambered eyes of vertebrates, both in their construction and their cellular components (Figure 1A). Nor are they related to the much better-known compound eyes of insects and crustaceans (Figure 1B). Their function has been a mystery, since they seem to be involved in neither defence nor predation. In a recent article Garm and Nilsson [1] have been able to show that, in the starfish *Linckia laevigata*, the eyes are used to locate large landmarks, specifically the dark edges of the coral reefs that they typically inhabit. Their vision is not good, with a minimum angle of resolution of 15–30° (compared with 1° for a bee and 1′ for a human). This enables the starfish to see a 1 metre high reef from 2 metre away, but not from 4 metres away. An interesting question that this poor performance raises is why some animal groups, like the starfish, evolved eyes but never developed them to a stage where they could become of more than minimal single-task use.

There are only three animal groups in which eyes have become general-purpose sensory instruments involved in many aspects of behaviour [2]. These are the cephalopod molluscs, the arthropods, and the vertebrates. If one considers the bee as an example, the eyes are used for navigation using celestial cues and landmarks, for recognising food plants by shape and colour, for flight control using a sophisticated motion-vision system, and for recognising other members of their own or other species for mating and defence. A similar catalogue can be drawn up for most vertebrates and cephalopod molluscs.

In other animal groups vision is present, but has not been exploited to the same degree, and in many cases it is used for only a single function. For example, in the bivalve molluscs several different kinds of eye have evolved for the sole purpose of defence: Nilsson [3] describes these as ‘burglar alarms’. Often these eyes are quite sophisticated: scallop eyes have unique concave mirror optics, the arc shells have small compound eyes around the mantle edge, and giant clams have pinhole eyes with modest resolution which nevertheless allow the animal to respond to a fish before it gets near enough to nibble the tentacles [4]. These all seem to be based on off-responding neurons that originally provided a shadow response: adding some optics allows the animals to respond to a predator before it is on top of them. Something similar happened in some sabellid tube-worms that have equipped themselves with compound eyes for the same defensive purpose.

‘Single-purpose’ eyes are not confined to use in defence: the alciopid annelids, pelagic worms that prey on other animals in the plankton, have evolved eyes with lenses that produce excellent images and would not disgrace a small fish. Similarly in the gastropod molluscs the heteropods have scanning eyes with large lenses which they again use to capture planktonic prey [5]. It is unlikely that these eyes are used for any other purposes.

Why did these eyes go nowhere beyond their one use? It is not because they were not up to the job: scallops have 2° resolution, and alciopid and heteropod eyes more like 1°, which is at least as good as most insects. It is not lifestyle either, as some of these animals are carnivores and others are

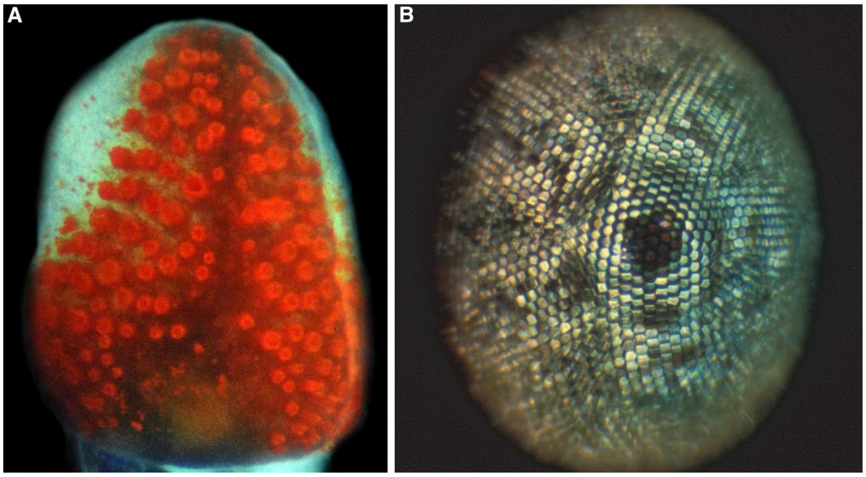

Figure 1. Compound eyes of a starfish and a crustacean.

(A) The eye of the starfish *Linckia laevigata* showing ommatidia without lenses in a loose irregular structure. Height 0.6 mm. (Reproduced with permission from [1].) (B) Eye of a hermit crab *Pagurus excavatus* showing ommatidia with complex optics in a tight hexagonal structure. Height 2 mm. (Courtesy of Dan-Eric Nilsson.)

filter feeders. If we compare them to the three major groups that have attained multipurpose vision, we find that what the latter have in common is a relatively large brain, and within that brain a huge proportion devoted to vision: rough estimates are 60% for man, 79% for a fly and 67% for an octopus [2].

In computational terms, sophisticated vision is not cheap. Typically such brains have partially separate pathways for pattern and for motion (corresponding roughly to the ventral and dorsal cortical streams in man [6]). This combination of mechanisms for recognition and for locomotor control presumably arose in all three lineages in the melting pot of the Cambrian. Thereafter it has been sufficiently adaptable to enable animals — in two of the three groups — to cope with life on land, and eventually with flight. In contrast, none of the animals with single-purpose vision has a particularly large brain, nor a high proportion devoted to vision.

Nilsson [7] has described vision in animals as arising in four evolutionary stages: first, simple photoreception; second, photoreception with some degree of directionality allowing basic phototaxis; third, low-resolution spatial vision; and fourth, high-resolution multipurpose vision. The starfish studied by Garm and Nilsson [1] fit firmly into the third category: they have spatial vision good enough to allow them to navigate towards large dark objects, but are probably used for little else. This third category is in a way the most heterogeneous and problematic. It contains animals as diverse as cubomedusan jellyfish which use low resolution vision to maintain station in water currents, copepods with tiny eyes that use vision for finding mates, and others such as *Nautilus* which has retained a very inefficient pinhole eye while its cephalopod relatives evolved excellent lens eyes [4]. In all these cases vision seems to have got stuck at some evolutionary stage, either because the animals had no need for better eyesight, or because their brains were not initially configured in a way that allowed it. It is something of a chicken and egg problem: did lack of visual capacity hold back behaviour, or was it the other way round?

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Genetics: A Common Origin for Neuronal Asymmetries?

A new study reveals an unexpected genetic link between two distinct types of neuronal asymmetries in the nematode *Caenorhabditis elegans*. This finding suggests a common origin of genetically determined asymmetries and raises intriguing questions about their evolution.

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The nervous system of most animals is overall bilaterally symmetric. However, a number of neural circuits show distinct proportions and/or types of neurons on the left and right sides [1]. Several types of neural asymmetries normally co-exist in an individual of a particular species. For example, humans exhibit circuit asymmetries within ascending (sensorial), descending (motor) and higher-order (associational and commissural) pathways [2], while various types of neuronal asymmetries are observed in the nervous system of *Caenorhabditis elegans* [3]. A recent study by Cochella *et al.* [4] has addressed whether — and to what extent — different types of neural asymmetries are linked in their origin by providing the first demonstration of a genetic link